Time since first naturalization is key to explaining non-native plant invasions on islands

Running title: Naturalization time drives island invasions

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Abstract

Aim

Investigating the extent of insular invasions by non-native species (i.e. the number of islands they occupy) is central to island conservation. However, interrelationships among plant life history traits, naturalization histories, and island characteristics in determining island occupancy by non-native plant species are poorly understood. We investigated whether island occupancy by different non-native plant species varies according to their year of first naturalization and whether periods of first naturalization differ across growth forms, dispersal modes, and biogeographic origins. Then, we asked if non-native plants that naturalized more recently occur more frequently on islands that are large, less isolated and close to urban areas. We contrasted trends across growth forms, dispersal modes and biogeographic origins.

Location

264 offshore islands in northern Aotearoa New Zealand

Taxa

Vascular plant species

Methods

We combined field surveys and published data for 767 non-native plant species. We categorized each species according to its growth form (n = 3), dispersal (n = 4) mode and biogeographic origin (n = 5) and identified its year of first naturalization in Aotearoa New Zealand. We tested our hypotheses using ANCOVA and generalized linear models (GLMs).

Results

There were similar relationships between island occupancy and year of first naturalization in Aotearoa New Zealand across all trait and biogeographic origin categories but there were distinctly different times of first naturalization within each category. First naturalization times of herbaceous species, those with unspecialized dispersal modes, and those originating from Eurasia and the Mediterranean basin were disproportionately earlier than other categories. Non-native plants with more recent first naturalization occur more frequently on large islands close to urban areas, but not on less isolated ones. Relationships with island characteristics did not differ among trait and biogeographic origin categories.

Main Conclusions

Overall, time of first naturalization is more important than trait and biogeographic origin categories in explaining non-native plant invasion patterns on islands. Since there were similar relationships between island occupancy and year of first naturalization in Aotearoa New Zealand for all categories, management bodies should focus on species of trait and biogeographic origin categories that naturalized more frequently in recent times (e.g. woody species from other regions within Oceania), and on large islands close to urban areas. Introduction and naturalization histories provide essential context for interpreting the role of plant traits and biogeographic origin in understanding plant invasions on islands.

Key Words: *Aotearoa New Zealand, Biogeographic origin, Dispersal modes, Growth forms, Island occupancy, Island biogeography, Naturalization time, Plant species*

Introduction

The introduction of non-native species poses considerable threats to islands' biodiversity (Dawson et al., 2017, Kueffer et al., 2010; Lonsdale, 1999; Pyšek & Richardson, 2006; Walentowitz et al., 2023). Given the large numbers of species introduced to islands (Sax & Gaines, 2008, Wilkinson 2004), understanding the extent of insular invasions (i.e. the number of islands occupied) and which island characteristics influence the spread of non-native species is central to island conservation (Lloret et al., 2005, Mologni et al., 2021; Moser et al., 2018). However, the interrelationships between these elements and introduction and naturalization histories and life history traits of non-native species remain poorly understood (Kinlock et al., 2022; Lloret et al., 2005; Schrader et al. 2021a).

Rates of non-native species naturalization have changed over time (Sax & Gaines, 2008), primarily because of varying introduction rates. The overall number of new species introduced worldwide remained relatively low until the 19th century (Seebens et al., 2017). After that, numbers largely increased, except for the period 1914–1945, marked by two major wars and rather constant introduction numbers (Pyšek et al., 2020; Seebens et al., 2017). After 1945, rates of non-native species introduction increased and are not slowing, correlated with increasing volumes of commerce worldwide (Pyšek et al., 2020; Seebens et al., 2017). Identifying the time of first introduction and naturalization and how they relate to later spread will help forecast future range expansions and guide management focused on early containment or eradication.

Species introduced earlier are likely to occupy a larger number of islands than recent introductions (Moyano et al., 2022). However, island colonization is also regulated by island characteristics (MacArthur & Wilson, 1967). Large islands offer a bigger target for dispersing propagules and therefore are more likely to be occupied first (i.e. target island effect, Lomolino, 1990). Similarly, less isolated islands are more easily reached by dispersing propagules and thus will be occupied before more isolated islands (MacArthur & Wilson, 1967 but see Moser et al., 2018). Since the introduction and naturalization of non-native plant species often rely on humans, islands that are inhabited or close to human communities are likely to be more readily invaded (Sullivan et al., 2005; Timmins & Williams, 1991, Walentowitz et al., 2023). Interactions between these determinants of island invasions and island occupancy by non-native plants have been rarely investigated.

Time of introduction and naturalization, island occupancy, and island characteristics that favour initial colonization of islands are likely to be related to plant life history traits. For instance, a disproportionate number of herbaceous European species were initially introduced in many parts of the world for agricultural purposes and in an attempt to “recreate” a landscape familiar to settlers (Crosby, 2004; Lenzner et al., 2022). Island occupancy might be higher for non-native plant species that disperse more efficiently, either because of shorter life cycles (e.g. herbs) or because of morphological adaptations allowing for long-distance dispersal (Arjona et al., 2018; Mologni et al., 2022; Negoita et al., 2016). Likewise, species originating from biogeographic areas with climates similar to the invaded range are likely to have an advantage when establishing new populations (Richardson & Pyšek, 2012). These traits might also affect how they relate to island characteristics. For instance, long-distance dispersal species might show weaker relationships with isolation (Arjona et al., 2018; Negoita et al., 2016), while high propagule pressure in species with short life cycles might mask a target island effect.

Here, we aim to better understand the role of naturalization histories and plant traits in explaining non-native plant invasions on islands. We calculated non-native plant species richness on 264 islands off the northern coast of Aotearoa New Zealand, for a total of 831 non-native vascular plant species. We asked: (1) Does island occupancy by non-native plant species vary according to year of first naturalization in Aotearoa New Zealand and, if so, is the relationship consistent across different growth forms, dispersal modes, and biogeographic origins? (2) Do periods of naturalization in Aotearoa New Zealand differ within and among different growth forms, dispersal modes and biogeographic origins? (3) If non-native plant species colonize larger, less isolated islands that are close to urban areas first, does the average (a) area, (b) isolation and (c) distance from urban areas of the islands where a species occurs respectively increase, decline and decline with its year of first naturalization? If so, do the relationships differ across growth forms, dispersal modes and biogeographic origins?

Methods

Study system

The study system comprises 264 islands off the northern coast of Aotearoa New Zealand's North Island (hereafter the 'mainland'). The study system spans six hundred kilometres (34–38 °S, 172–179 °E, Figure 1). The islands vary in area from 0.00002 to 277.21 km^2, and range from islands connected to the mainland at low tides to those >50 km from the coast (Mologni et al. 2022). Most are land-bridge islands that were connected to the mainland during the last glacial maximum (Poor Knight Islands excepted, Fleming, 1979). They supported warm temperate rain forests (sensu Grubb et al., 2013) before human settlement (circa 740 years ago, Wilmshurst et al., 2014). Humans cleared, burned and farmed many islands (Bellingham et al., 2010), some of which were abandoned in only the last few decades. Northern Aotearoa New Zealand is the most populous region of the country

(Statistics NZ Tatauranga Aotearoa, 2018), and 41 islands are still inhabited within the study system.

Data collection

The total number of non-native vascular plant species occupying each of the 264 islands was quantified by collating previously published material and field surveys (see Mologni et al., 2021 for more details). We obtained permits for all unpublished surveys by either the New Zealand's Department of Conservation or Māori and private island owners. For each species, we obtained the year of their first naturalization from the New Zealand Plant Conservation Network and Gatehouse (2008). Of the 831 non-native species, only 767 were included in our analyses. Thirty-three were removed due to taxonomic uncertainty, while 31 were not included due to a lack of first-naturalization data.

We classified non-native species according to their growth form, dispersal mode and biogeographic origin (Table 1). Four categories of growth forms were identified: graminoids, forbs, woody species, and lianas and climbers. Five categories of dispersal modes were defined based on morphological adaptations to long-distance dispersal: wind-, water-, animal-dispersed, unspecialized and short-distance (Arjona et al., 2018; Burns, 2019; Mologni et al., 2022; Negoita et al., 2016). Nine categories of biogeographic origin were delineated: Cosmopolitan, Eurasian (excl. Mediterranean basin), Mediterranean (i.e. Mediterranean basin), Tropical, Southern African, Oceanian (excluding Aotearoa New Zealand, and mainly Australian), North American (i.e. species restricted to North America), Other American (i.e. species ranging across all America or temperate South America) and Macaronesian (see Table 1 for more details). All species could be categorized based on their growth forms; however, 18 and 33 species were respectively excluded from dispersal mode and biogeographic origin analyses due to a lack of data. Of these categories, six were removed due to the small sample size: lianas and climbers (number of species = 40), water-dispersed (n = 16), cosmopolitan (n = 36), North American (n = 31), Other American (n = 15), Macaronesian (n = 5). In total, we used 3 categories for growth forms, 4 for dispersal modes and 6 for biogeographic origins (Table 1). Species were categorized by consulting Acta Plantarum (2007), Brandt et al. (2021), and the New Zealand Plant Conservation Network (2023), in addition to our professional expertise.

Island characteristics were quantified using ArcGIS 10.5.1 (ESRI, 2011). The size of an island was calculated as the total surface area in km^2. Isolation was measured as the total amount of water surrounding each island (Carter et al., 2020; Diver, 2008; Negoita et al., 2016). The greater the amount of water, the more isolated an island is. For each island, we created several concentric buffers with radii of 250, 500, 1000, 1500, 2000, 2500 and 3000 m. Then, we calculated the amount of water within each radius (%). To quantify the effect of isolation from human communities, we calculated the shortest distance from the nearest urban area (m). We defined as urban built-up areas having a population of 1000 people or more (Statistics NZ Tatauranga Aotearoa, 2018).

Statistical analyses

To test whether island occupancy varies according to year of first naturalization and across growth forms, dispersal modes, and biogeographic origins, we used a generalized linear model (GLM). We set the number of islands occupied by each species as the dependent variable and their year of first naturalization time in Aotearoa New Zealand as the independent variable. Since the dependent variable was right-skewed even after transformation, we modelled data using linear, quasipoisson and negative binomial models for all species. Results were consistent and, for simplicity, we opted for a linear model. We assessed differences in slopes among different trait and biogeographic origin categories with

ANCOVA tests. The number of occurrences was log-transformed in all linear models to conform to assumptions of normality.

To test whether non-native species show distinct periods of their naturalization across growth forms, dispersal modes, and biogeographic origins, modes were extracted for each trait and biogeographic origin category after binning the year of naturalization by 20-year periods. Additionally, we contrasted the distribution of each category of growth forms, dispersal modes and biogeographic origin using ANOVAs.

To test whether non-native plants that naturalized more recently occur more frequently on islands that are large, less isolated and close to urban areas, we set the average area, isolation and distance from urban areas of occupied islands by each species as the dependent variables in three separate linear models. The years of first naturalization in Aotearoa New Zealand was used as the independent variable. To conform to assumptions of normality, the average area, isolation and distance from urban areas of occupied islands were respectively log-, arcsine- and square root-transformed. Tests were run for all species first, then ANCOVA tests were used to contrast slopes among different trait and biogeographic origin categories. All analyses were conducted in R (R Core Team, 2023). A post hoc Tukey test and Bonferroni correction were applied for multiple testing at all stages (Hothorn et al., 2008).

Results

The earlier a non-native plant species had naturalized in Aotearoa New Zealand, the more islands it occupies (Figure 1 & Table S1). However, the slopes of relationships between the number of islands occupied and year of first naturalization did not differ significantly among different non-native plant growth forms, dispersal modes or biogeographic origins (Table S2).

The non-native plant species on the islands had mainly two 20-year bin periods of peak naturalization – 1850 to 1870 and 1970 to 1990 (Figure 2, Table 2 & Table S3). Non-native graminoids and forbs on the islands had disproportionately first naturalized in Aotearoa New Zealand between 1850–1870, whereas woody species had disproportionately first naturalized between 1970–1990 (Figure 2, Table 2 & Table S3). Differences between non-native woody species and other growth forms were significant, as were differences between forbs and graminoids (ANOVA and Tukey tests: Table S4). Among dispersal modes, unspecialized and animal-dispersed species on the islands had disproportionately first naturalized in Aotearoa New Zealand between 1850–1870, whereas short-distance species had disproportionately first naturalized between 1970–1990 (Figure 2, Tables 2 & Table S3). Wind-dispersed species first naturalized disproportionately 1930–1950 (Figure 2, Tables 2 & Table S3). Differences between unspecialized species and other dispersal modes were significant (ANOVA and Tukey tests: Table S4). Non-native Eurasian and Mediterranean plant species on the islands had disproportionately first naturalized during1850–1870, those from Southern Africa in both 1930–1950 and 1970–1990, and those from Oceania and tropical regions during 1970–1990 (Figure 2, Table 2 & Table S3); there was a significant difference in first naturalization dates between Eurasian and Mediterranean species and those from other biogeographic regions (ANOVA, Tukey tests: Table S4).

The average area and distance from urban areas of islands where a species occurred respectively increased and declined with year of first naturalization (Table 3). No significant relationship was detected between the average isolation of islands where a species occurred and year of first naturalization (Table 3). There were no significant differences in non-native plants’ growth forms, dispersal modes and biogeographic origins for the average area, isolation and distance from urban areas of islands where a species occurred (Table 3 & Table S5).

Discussion

We found similar negative relationships between island occupancy and year of first naturalization across growth forms, dispersal modes, and biogeographic origins of non-native plants on islands in northern Aotearoa New Zealand. We also identified differences in periods of first naturalization in Aotearoa New Zealand among growth forms, dispersal modes and biogeographic origins. Consistent with studies in the same system (Mologni et al., 2021), large islands close to urban areas were more frequently colonized first by invading species. However, once the year of first naturalization was accounted for, and in contrast to an earlier study (Mologni et al., 2022), there were no differences across categories of growth forms, dispersal modes and biogeographic origin.

Once the year of naturalization was accounted for, it was a better predictor than life history traits in explaining non-native plant invasions on the islands. Date of first naturalization has previously been identified as a crucial factor in explaining non-native plant invasions (Fristoe et al., 2021, Moyano et al., 2022) but the interrelationship between time of naturalization and plant traits as a predictor of invasion success on islands has been little explored (but see Moyano et al., 2022). In our study, non-native woody plant species have colonized proportionately fewer islands but most of them have naturalized more recently than other growth forms. Herbaceous species used for agriculture were introduced and naturalized disproportionately early, whereas woody, ornamental species have naturalized disproportionately recently (Gatehouse, 2008). Among dispersal modes, more unspecialized plant species naturalized early, perhaps reflecting a higher efficiency in exploiting human-related pathways. Among biogeographic origins, more plant species from Eurasia and the Mediterranean naturalized early, a reflection of European settlement (Gatehouse, 2008; Lenzner et al., 2022). In particular, species originating from other regions within Oceania (mostly Australian species) are disproportionately woody (60.3%, see Table S6), and these species might be a particular focus for elimination for managers seeking to reduce invasions on the islands in our study system.

If species occupy a similar number of islands irrespective of trait and biogeographic origin categories, we might expect that, in time, more non-native woody species will invade more islands, as the earlier-naturalized herbaceous species have already done (Howell, 2019). Even so, woody species may show longer time lags since they will be generally slower to reach reproductive maturity than herbaceous species (Grime, 2002). In support of this view, there have been few introductions of new non-native conifer species to Aotearoa New Zealand since its 1993 Biosecurity Act significantly reduced introduction rates of non-native species (Seebens et al., 2017). Nonetheless, their naturalization has continued at a linear rate to the present (Howell, 2019), potentially because some species introduced before 1993 reached reproductive maturity only recently, although other factors, such as recent co-invasions by mutualists, can also determine more recent invasions by woody plants (Gardner & Early, 1996, Dickie et al., 2010). Similar trends might be expected for other categories that were more consistently introduced in recent times.

Previous work in the study system found that graminoids and long-distance dispersal species have higher occupancy of islands than other trait categories (Mologni et al., 2022). However, despite their higher occupancy of islands, graminoids and long-distance dispersal species are no different in their relationship between year of first naturalization and island occupancy than other life forms and dispersal modes. This implies they require a similar amount of time to other categories for island colonization. Other processes might explain why they occupy more islands in our study system. For instance, they might have been purposely introduced more consistently than other categories. Alternatively, species introduced and naturalized early might negatively impact the establishment of other non-native species (i.e.

priority effect, Fraser et al., 2015, Catford et al., 2022). For instance, herbaceous European and Mediterranean non-native species that naturalized early and invaded the islands might reduce the probability of successful establishment by herbaceous non-native species from other biogeographic regions through niche pre-emption (Fukami, 2015). Notably, European sward-forming grasses were introduced and naturalized in the mid-19th century (Allan, 1936) and, in exposed perimeters of islands, these grasses can be effective barriers to colonization by other native and non-native plants (Esler, 1988, Richardson et al., 2018).

Non-native plants that naturalized more recently occurred more frequently on large islands, consistently with the target island effect (Lomolino, 1990). However, large islands in the region are also inhabited (Mologni et al., 2021). Whether the more consistent colonization of large islands reflects autonomous or human-mediated dispersal is unclear, both processes though are likely at play. Since they both increase the likelihood of large over small island colonization, island area might then simultaneously encapsulate a “geographic” target island effect (i.e. species colonize larger islands first because they offer a bigger target) and a “human-mediated” target islands effect (i.e. human inhabit larger islands, disproportionately introducing non-native species). For example, the first invasions of the palm *Archontophoenix cunninghamiana* (native to Australia, first naturalized in 1992) on large, inhabited islands almost certainly derived from gardens in which it was widely planted in the 1980s–1990s (Cameron, 2000; Sullivan et al., 2005) but its wider bird dispersal into natural forests (Christianini, 2006, Sheppard, 2013) is likely to have resulted in its wider invasion on those islands and from them to other islands.

Non-native plants that naturalized more recently did not occur more frequently on less isolated islands. However, a negative effect of isolation on non-native species richness was previously identified (Mologni et al., 2021). Perhaps this pattern is simply more difficult to capture, and, over time, less isolated islands still accumulate more species than more isolated islands through multiple colonization events. In contrast, non-native plants that naturalized more recently occurred more frequently on islands that are close to urban areas. Since non-native species often use human-related pathways (Pyšek et al., 2020; Sinclair et al., 2020), islands close to urban areas are more likely to be colonized just by proximity (Sullivan et al., 2005; Timmins & Williams, 1991). For non-native species in this study system, isolation might be more strongly associated with humans than with geography.

The relationships between island characteristics and time since first naturalization were similar across trait and biogeographic origin categories. This suggests that the same processes regulate the initial colonization of these islands, irrespective of plant life history traits. This is surprising since a growing body of literature has identified differences in island species distributions based on traits (Conti et al., 2022; Mologni et al., 2022; Schrader et al., 2021b; Schrader et al., 2023; Walentowitz et al., 2022). Alternatively, other traits might be more important. For instance, wind-pollinated species are independent of biological carriers for dispersing their pollen, an advantage in newly occupied islands (Cox et al., 1997). Propagule pressure is another trait that likely influences the ability to rapidly colonize more islands (Lockwood et al., 2005). Future studies should assess a broad suite of traits when assessing island invasion.

The year of naturalization was used to identify periods of non-native plant species' naturalizations. However, in many cases, long periods of time can elapse between the introduction, naturalization and identification of newly naturalized species. This is particularly important for earlier introductions, more likely to go unnoticed due to a lack of awareness of biological invasions. Conversely, we can expect current monitoring activities to be more effective in identifying new non-native species (Pyšek et al., 2020). Unfortunately, accounting for this form of error will be challenging.

Since similar relationships between island occupancy and year of first naturalization were identified for all trait and biogeographic origin categories despite different periods of naturalization, management bodies should focus on species of categories that naturalized more frequently in recent times, such as woody species (Howell, 2019) originating from other regions within Oceania and short-distance dispersal species, and on large islands close to urban areas. Additionally, this work builds on and aligns with a growing body of literature implementing traits in island biogeography (Ottaviani et al., 2020; Schrader et al., 2023; Whittaker et al., 2014), and shows that introduction and naturalization histories provide essential context for interpreting the role of plant traits and biogeographic origin in understanding plant invasions on islands.

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Data availability statement

Data are available as supplementary material. Island locations (longitude and latitude) are not publicly available due to private ownership and issues of data sovereignty of concern to Māori.

Tables

Table 1 Description and the number of species for growth form, dispersal mode and biogeographic origin categories across 264 Aotearoa New Zealand offshore islands.

Category	**Description**	**Number of species**
Growth forms		**767**
Graminoids	Grasses, sedges and rushes	120
Forbs	Herbaceous, non-graminoid	466
Woody species	Trees and shrubs	141
Climbers and lianas	Herbaceous or woody climbers	40
Dispersal modes		**749**
Wind-dispersed	Plumes, wings, dust diaspores (anemochory)	139
Water-dispersed	Buoyant propagules, e.g. corky tissues, air pockets (hydrochory)	16
Animal-dispersed	Fleshy fruits or adhesive barbs (endo and epizoochory)	155
Unspecialized	No evident or prevalent morphological adaptations (unspecialized)	281
Short-distance	Morphological adaptations for short-distance dispersal only (ballochory, myrmecory)	158
Biogeographic origin		**734**
Eurasian	Europe (excl. Mediterranean basin), Asia, North Africa and the Arabian Peninsula	302
Cosmopolitan	Cosmopolitan, subcosmopolitan and temperate areas of the northern hemisphere	36
Other American	All America (North, Central, South) or Temperate South America	15
Mediterranean	Mediterranean basin	94
North American	Nearctic	31
Oceanian	Australia, Pacific	61
Southern African	South Africa, Eswatini, Lesotho, and Namibia	66

Tropical	Tropical Africa, Asia, Central and South America, Madagascar and Pantropical	124
Macaronesian	Macaronesia	5

Table 2 Peak of naturalization (mode) and the number of species introduced per 20-year bin period for growth form, dispersal mode and biogeographic origin categories across 264 Aotearoa New Zealand offshore islands.

Category	**Peak of naturalization (Mode)**	**Number of species introduced**
Growth forms		
Graminoids	1850–1870	34
Forbs	1850–1870	129
Woody species	1970–1990	49
Dispersal modes		
Wind-dispersed	1930–1950	27
Animal-dispersed	1850–1870	37
Unspecialized	1850–1870	89
Short-distance	1970–1990	34
Biogeographic origin		
Eurasian	1850–1870	100
Mediterranean	1850–1870	27
Oceanian	1970–1990	20
Southern African	1930–1950, 1970–1990	15, 15
Tropical	1970–1990	27

Table 3 Top section: separate linear relationships between the average area, isolation and distance from urban areas (average urban) of occupied islands and year of first

naturalization across all species. Entries are model, estimate, t- and p-value. Bottom section: Interaction terms extracted from ANCOVA models between the average area, isolation and distance from urban areas (average urban) of occupied islands and time since first naturalization by growth forms, dispersal modes and biogeographic origin. Entries are model, sum of squares, F- and p-value. P-values are in bold when significant (<0.05).

Overall models			
Model	**Estimate**	**t-value**	**p-value**
log (average area) ~ year of first naturalization	0.00 ± 0.00	3.68	**<0.001**
arcsine (average isolation) ~ year of first naturalization	-0.00 ± 0.00	0.44	0.662
square root (average urban) ~ year of first naturalization	-0.25 ± 0.03	-7.60	**<0.001**
Interaction terms			
Model	**Sum of squares**	**F-value**	**p-value**
log (average area) ~ year of first naturalization * growth forms	3.60	1.72	0.180
log (average area) ~ year of first naturalization * dispersal modes	8.30	2.55	0.054
log (average area) ~ year of first naturalization * biogeographic origin	3.40	0.78	0.536
arcsine (average isolation) ~ year of first naturalization * growth forms	0.04	0.67	0.513
arcsine (average isolation) ~ year of first naturalization * dispersal modes	0.15	1.60	0.188
arcsine (average isolation) ~ year of first naturalization * biogeographic origin	0.15	1.23	0.295
square root (average urban) ~ year of first naturalization * growth	3346.00	0.90	0.406
square root (average urban) ~ year of first naturalization * dispersal	9098.00	1.54	0.203
square root (average urban) ~ year of first naturalization * biogeographic origin	14467.00	1.93	0.105

Figure Captions

[single column] Figure 1 Relationships between the number of islands occupied by a species and their year of first naturalization for growth form (top), dispersal mode (centre) and biogeographic origin (bottom) categories across 264 Aotearoa New Zealand offshore islands. No statistical differences were identified in contrasting categories.

[double column] Figure 2 Frequency plots displaying the number of species naturalized per 20-year bin period for growth form (top), dispersal mode (centre) and biogeographic origin (bottom) categories across 264 Aotearoa New Zealand offshore islands. Numbers illustrate the number of species introduced at the mode (naturalization peak) by category. Two modes were identified for Southern African species.

Figure 1

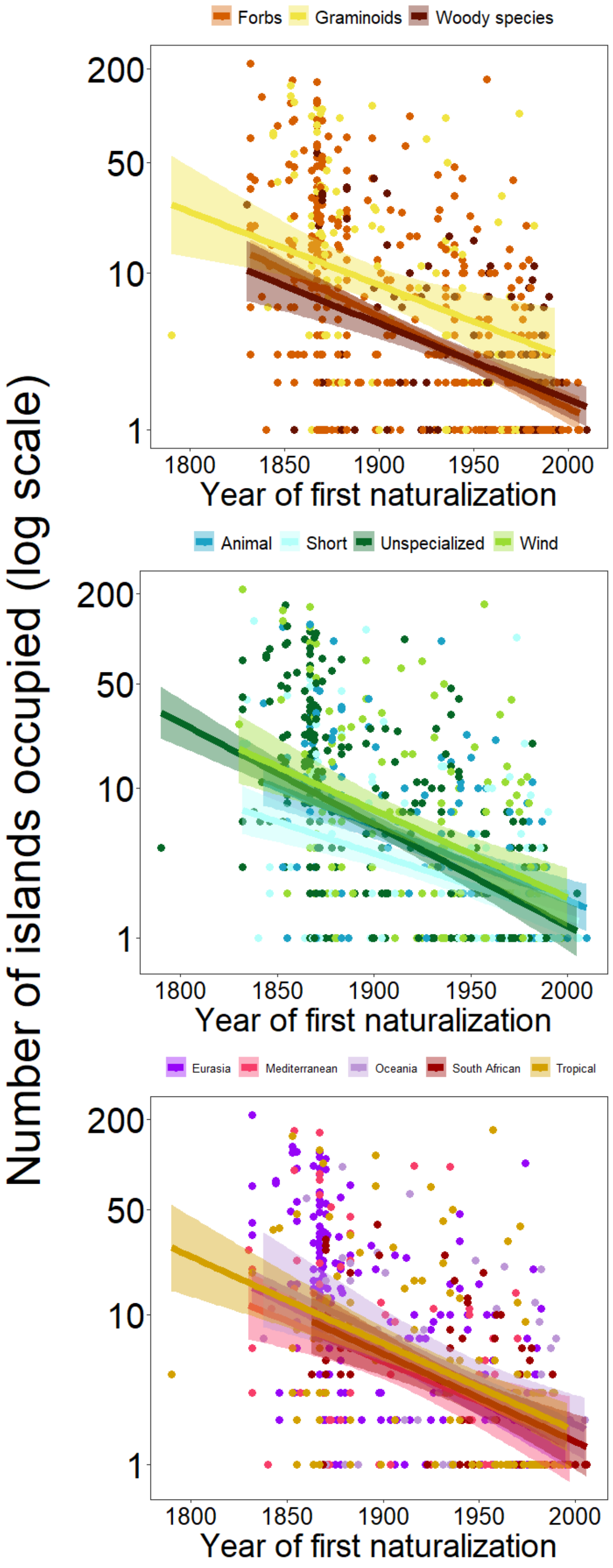
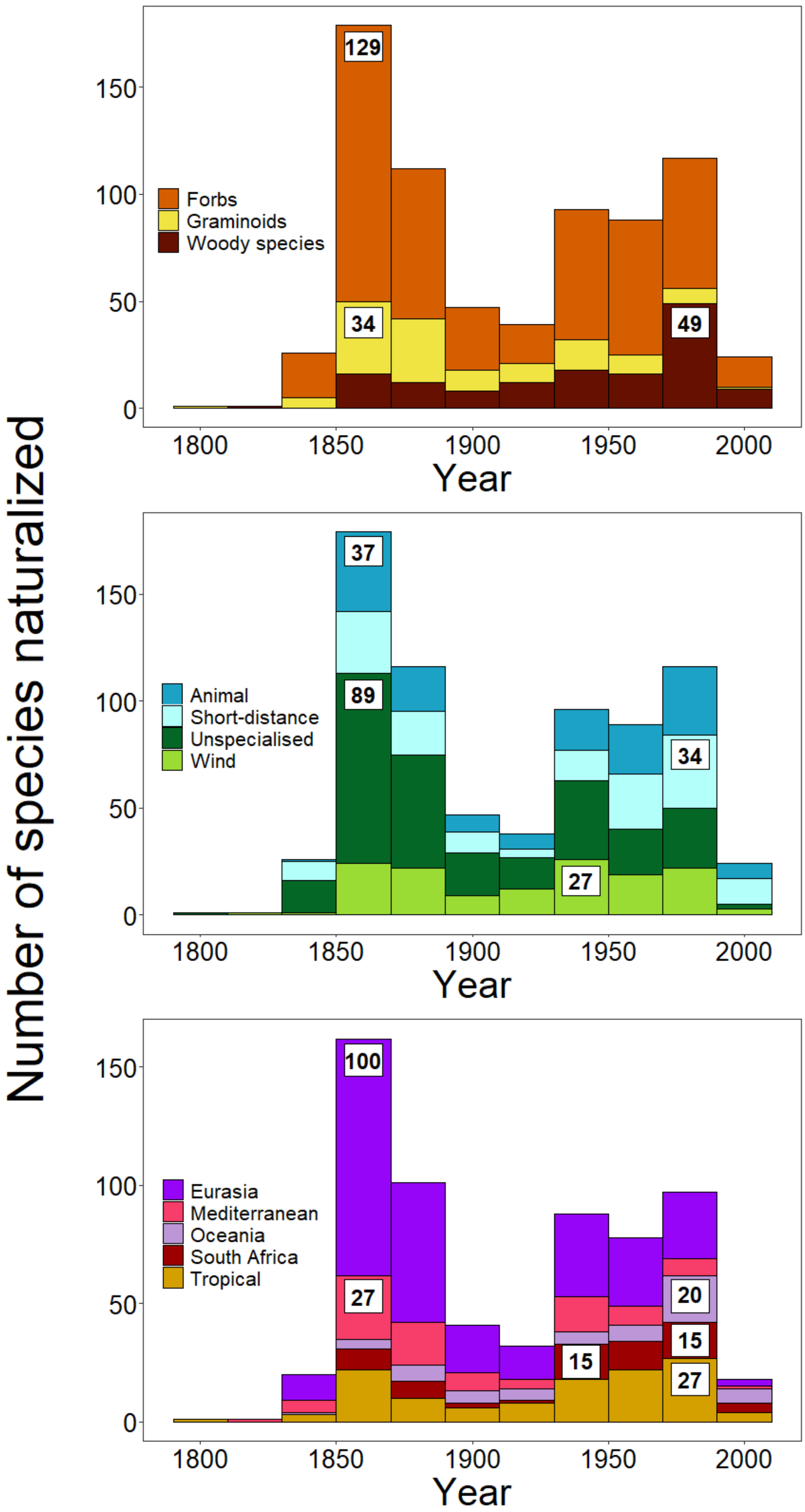

Forbs
Graminoids
Woody species
Animal
Short
Unspecialized
Wind
Eurasia
Mediterranean
Oceania
South African
Tropical
Number of islands occupied (log scale)
200
50
10
1
1800
1850
1900
1950
2000
Year of first naturalization

Figure 2


Number of species naturalized
150
100
50
0
Forbs
Graminoids
Woody species
129
34
49
1800
1850
1900
1950
2000
Year
150
100
50
0
Animal
Short-distance
Unspecialised
Wind
37
89
27
34
1800
1850
1900
1950
2000
Year
150
100
50
0
Eurasia
Mediterranean
Oceania
South Africa
Tropical
100
27
15
20
15
27
1800
1850
1900
1950
2000
Year